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Fourier Transform Infrared and Raman Spectroscopy for Characterization of *Listeria monocytogenes* Strains

Astrid Oust,[1,2]* Trond Møretrø,[1] Kristine Naterstad,[1] Ganesh D. Sockalingum,[3] Isabelle Adt,[3] Michel Manfait,[3] and Achim Kohler[1]

Matforsk AS, Norwegian Food Research Institute, Osloveien 1, N-1430 Ås, Norway[1]; Department of Chemistry, Biotechnology and Food Science, Norwegian University of Life Sciences, P.O. Box 5003, N-1432 Ås, Norway[2]; and Unité MéDIAN, UMR CNRS 6142, IFR 53, UFR de Pharmacie, Université de Reims-Champagne-Ardenne, 51 rue Cognaq Jay, 51096 Reims Cedex, France[3]

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The purpose of this study was to characterize the variation in biochemical composition of 89 strains of *Listeria monocytogenes* with different susceptibilities towards sakacin P, using Fourier transform infrared (FTIR) spectroscopy and Raman spectroscopy. The strains were also analyzed using amplified fragment length polymorphism (AFLP) analysis. Based on their susceptibilities to sakacin P, the 89 strains have previously been divided into two groups. Using the FTIR spectra and AFLP data, the strains were basically differentiated into the same two groups. Analyses of the FTIR and Raman spectra revealed that the strains in the two groups contained differences in the compositions of carbohydrates and fatty acids. The relevance of the variation in the composition of carbohydrates with respect to the variation in the susceptibility towards sakacin P for the *L. monocytogenes* strains is discussed.

The food-borne pathogenic bacterium *Listeria monocytogenes* represents a major concern with respect to food safety, especially because the bacterium is able to grow in refrigerated ready-to-eat products with an extended shelf life, a consumer product type with increasing popularity (25). Bacteriocins are antibacterial peptides produced by certain bacteria—for example, lactic acid bacteria (LAB)—in order to kill or inhibit the growth of other closely related bacteria (4). LAB have been used for the production and preservation of food for a long time, and since both the bacteria and their bacteriocins have been consumed for centuries, they are generally regarded as safe to eat. Thus, it has been suggested that the growth of *L. monocytogenes* in food might be limited by the addition of bacteriocins and/or bacteriocin-producing LAB (16). This suggestion has been supported by the results of several studies (8, 9). Katla et al. (10) investigated 200 strains of *L. monocytogenes* isolated from food or food-processing facilities for their susceptibilities towards four bacteriocins produced by LAB, among them sakacin P, which is a class IIa bacteriocin (15). The results showed that the different strains had different susceptibilities to the various bacteriocins. The reason for this variation is unknown, but if bacteriocins and/or bacteriocin-producing LAB are to be used as protective cultures against *L. monocytogenes*, it is important to understand the basis for this variation in order to certify the effects of these protective agents. A previous investigation of *L. monocytogenes* strains that were resistant to class IIa bacteriocins suggested that the resistance was coupled to several changes in the cell surfaces of the bacteria (26).

Fourier transform infrared (FTIR) spectroscopy and Raman spectroscopy are chemical analytical methods that have also been used to collect information about whole bacterial cells (14). The outputs from these methods are FTIR and Raman spectra that contain signals from the organic functional groups in the sample. Since the bands in FTIR spectra are due to polar functional groups while the bands in Raman spectra are due to nonpolar functional groups, FTIR and Raman spectroscopy are complementary techniques. Many of the functional groups seen in bacterial FTIR and Raman spectra can be attributed to specific biomolecules (proteins, lipids, carbohydrates, and nucleic acids), and therefore valuable information about the biochemical composition of the bacteria can be obtained (3, 22, 23, 27).

The aim of this work was to study the biochemical basis for the variation in susceptibility towards bacteriocins for strains of *L. monocytogenes*. This was done using FTIR spectroscopy and Raman spectroscopy to investigate the variation in the biochemical compositions of strains of *L. monocytogenes* with different susceptibilities to sakacin P.

MATERIALS AND METHODS

Strains and background information. Katla et al. (10) characterized 200 strains of *L. monocytogenes* with respect to their susceptibilities to sakacin P. When the susceptibilities of the 200 strains were plotted in decreasing order, the strains formed two groups, susceptibility group A and susceptibility group B, separated by a gap in susceptibility values between them. Of these 200 strains, the following 89 were selected for analysis by FTIR spectroscopy (Table 1): the 20 strains closest to the sakacin P susceptibility gap, the 10 strains which are most susceptible to sakacin P, and the 10 strains which are least susceptible to sakacin P, with the remaining 49 strains being selected to cover the regions between the extreme points and the gap. The 20 strains closest to the sakacin P susceptibility gap were also analyzed using Raman microspectroscopy (Table 1).

Sample preparation and FTIR measurements. For FTIR spectroscopy measurements, the strains were streaked out on tryptic soy agar (Oxoid, Basingstoke, United Kingdom), using a three-quadrant streak pattern, and incubated at 30°C for 24 h. After cultivation, the samples were prepared, and FTIR spectra were acquired as described by Oust et al. (17), based on a procedure described by

* Corresponding author. Mailing address: Matforsk AS, Norwegian Food Research Institute, Osloveien 1, N-1430 Ås, Norway. Phone: 47 64 97 01 00. Fax: 47 64 97 03 33. E-mail: astrid.oust@matforsk.no.

TABLE 1. *Listeria monocytogenes* strains used for this study[a]

Strain[b]	Susceptibility to sakacin P (IC_{50} value) (ng/ml)[c]	Sakacin P group	FTIR group	AFLP group	Serogroup[d]	Strain[b]	Susceptibility to sakacin P (IC_{50} value) (ng/ml)[c]	Sakacin P group	FTIR group	AFLP group	Serogroup[d]
779	0.0085	A	B	A	1/2	3477*	0.0545	B	B	B	1/2
1207	0.0098	A	A	A	4	1037*	0.0567	B	B	B	1/2
196	0.0098	A	A	A	4	1348*	0.0567	B	B	B	1/2
228	0.0100	A	A	B	4	3035*	0.0614	B	B	B	1/2
1267	0.0102	A	B	A	1/2	2778*	0.0627	B	B	—[e]	1/2
1036	0.0104	A	B	A	1/2	3591*	0.0632	B	B	B	1/2
700	0.0110	A	A	A	4	1297	0.0682	B	B	B	1/2
187	0.0122	A	A	A	4	3078	0.0724	B	B	B	1/2
1293	0.0123	A	B	A	1/2	1185	0.0798	B	B	B	1/2
1272	0.0125	A	A	A	4	1461	0.0887	B	B	B	1/2
2842	0.0131	A	B	A	1/2	2340	0.0922	B	B	B	1/2
1603	0.0134	A	A	A	4	726	0.0983	B	B	B	1/2
2606	0.0136	A	B	A	1/2	1050	0.1014	B	B	B	1/2
1474	0.0142	A	A	A	1/2	1423	0.1051	B	B	B	1/2
193	0.0142	A	A	A	4	2830	0.1097	B	B	B	1/2
3135	0.0145	A	A	A	1/2	1355	0.1145	B	B	B	1/2
182	0.0158	A	A	A	4	1059	0.1232	B	B	B	1/2
50	0.0162	A	A	A	4	2301	0.1290	B	B	B	1/2
1425	0.0170	A	A	A	4	3052	0.1316	B	B	B	1/2
36	0.0173	A	B	A	1/2	2312	0.1417	B	B	B	1/2
913	0.0184	A	B	B	1/2	694	0.1487	B	B	B	1/2
969	0.0184	A	A	A	4	1199	0.1556	B	B	B	1/2
3152	0.0196	A	A	A	1/2	255	0.1610	B	B	B	4
1198	0.0197	A	A	A	4	830	0.1659	B	B	B	1/2
3138	0.0202	A	A	B	1/2	2816	0.1728	B	B	B	1/2
1308	0.0205	A	B	A	1/2	508	0.1760	B	A	B	4
2007	0.0214	A	A	A	4	2419	0.1830	B	B	B	1/2
673	0.0220	A	B	A	1/2	388	0.1953	B	B	B	1/2
686	0.0225	A	B	A	1/2	1437	0.2049	B	B	B	1/2
1331	0.0231	A	A	A	4	2499	0.2119	B	B	B	1/2
2455	0.0245	A	A	A	1/2	1317	0.2317	B	B	B	1/2
290*	0.0249	A	A	A	4	2786	0.2373	B	B	B	1/2
1419*	0.0254	A	A	A	1/2	1306	0.2487	B	B	B	1/2
39*	0.0254	A	A	A	1/2	857	0.2604	B	B	B	1/2
762*	0.0260	A	B	B	1/2	1295	0.2624	B	A	B	1/2
2014*	0.0266	A	A	A	1/2	1491	0.2685	B	B	B	1/2
688*	0.0269	A	A	A	1/2	1477	0.2752	B	B	B	1/2
2010*	0.0278	A	A	A	1/2	2420	0.2807	B	B	B	1/2
2114*	0.0289	A	A	A	1/2	1399	0.2886	B	B	B	1/2
3140*	0.0298	A	A	B	1/2	1334	0.3086	B	B	B	1/2
40*	0.0303	A	A	A	1/2	852	0.3233	B	B	B	1/2
921*	0.0494	B	B	B	1/2	20	0.3311	B	B	B	1/2
3066*	0.0504	B	B	B	1/2	1310	0.3634	B	B	B	1/2
701*	0.0525	B	B	B	4	1040	0.5983	B	B	A	1/2
502*	0.0528	B	B	B	1/2						

[a] All strains were measured by FTIR spectroscopy and AFLP. The 20 strains marked with asterisks were also measured by Raman spectroscopy.
[b] The strains were isolated by Aase et al. (1).
[c] The 50% inhibitory concentration (IC_{50}) values were determined by Katla et al. (10).
[d] Serogrouping was performed as described previously (19).
[e] For strain 2778, no result was obtained due to experimental error.

Helm et al. (7). For each strain, FTIR spectra were acquired from three independently cultivated bacterial samples, resulting in three parallel FTIR spectra for each strain.

Sample preparation and Raman measurements. For Raman microspectroscopy measurements, which for simplicity will be referred to as Raman spectroscopy, the bacteria were grown on tryptic soy agar at 30°C for 24 h. The bacterial biomass from each agar plate was dissolved in 1 ml of distilled water before centrifugation at 2,400 × *g* for 5 minutes. The cell pellet was transferred to a ZnSe crystal and divided into three deposits. The deposits were dried before spectra were collected using a Raman microspectrometer (Lab Ram; Jobin-Yvon–Horiba Raman Division, Lille, France) (18). The 785-nm radiation from an Ar^+-pumped Ti-Sa laser (Spectra Physics, Les Ulis, France) was used for excitation in combination with a 100× objective of an Olympus BX41 microscope (Olympus, France) for focus and collection of Raman scattered light. The confocal hole was set to 150 μm. Under these conditions, the power at the sample was about 60 mW. The spectral range was 2,000 to 400 cm^{-1}, which was covered using two measurement windows, with an accumulation time of 15 seconds for each and a grating of 950 lines/mm. All data acquisition and control of experimental parameters were carried out using LabSpec 4.03 (Jobin-Yvon-Horiba, France). For each strain, Raman spectra were acquired from two independently cultivated bacterial samples, resulting in six Raman spectra for each strain.

Preprocessing of FTIR and Raman spectra. The FTIR spectra were preprocessed by calculating the second derivative, using a second-order Savitzky-Golay algorithm with nine smoothing points (7, 21), before application of extended multiplicative signal correction (EMSC) (12) in the range from 3,200 to 720 cm^{-1}. The range from 3,200 to 720 cm^{-1} was used because this range contains most of the variation in the bacterial FTIR spectra. The purpose of calculating the second derivative was to remove broad underlying contours in the spectra due, for example, to water. EMSC on the second derivative spectra was applied to remove multiplicative effects (11, 12).

The Raman spectra were preprocessed using EMSC in the range from 1,770 to 600 cm^{-1}. EMSC was run in the range from 1,770 to 600 cm^{-1} because above

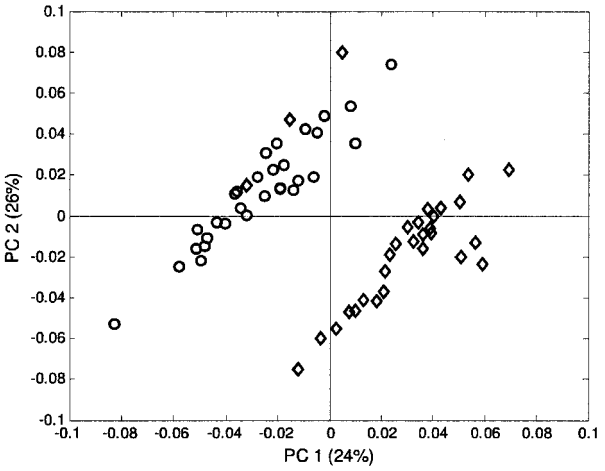

FIG. 1. Score plot for PCA of FTIR spectra (1,780 to 720 cm^{-1}) of 10 *Listeria monocytogenes* strains each from susceptibility groups A and B that are closest to the sakacin P susceptibility gap (10). All three parallel FTIR spectra for each strain were included in the PCA. The strains marked with diamonds are from susceptibility group A, while the strains marked with circles are from susceptibility group B.

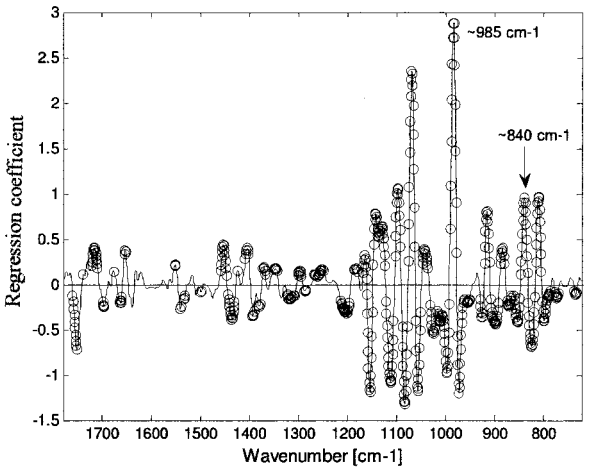

FIG. 2. Plot of regression coefficients from PLSR, with FTIR spectra (1,780 to 720 cm^{-1}) of 20 strains of *Listeria monocytogenes* as x and an indicator variable for the differentiation of spectra from susceptibility groups A and B as y (PLSR model 2). Significant regression coefficients are marked with circles. The bands at 985 cm^{-1} and 840 cm^{-1} were two of several significant bands for differentiation of the two susceptibility groups.

1,770 cm^{-1}, there are no valuable signals, while the range below 600 cm^{-1} contains signals from a filter in the Raman instrument.

Data analysis. The FTIR and Raman spectra were analyzed using principal component analysis (PCA) and partial least-squares regression (PLSR) (13). PCA was used to visualize the main variation and to detect clusters among the samples in the data set based on the FTIR/Raman spectra. PLSR was used to study the correlation between the variation in the FTIR/Raman spectra and other phenotypic knowledge about the *L. monocytogenes* strains. The optimal number of PLSR components and the significant variables in the PLSR models were calculated as described by Oust et al. (17). P values below 0.05 were regarded as significant. Data analysis was performed with Unscrambler 9.1 (Camo, Trondheim, Norway).

AFLP analysis. Amplified fragment length polymorphism (AFLP) analysis is a fingerprinting method used to study genetic diversity. The 89 *L. monocytogenes* strains were analyzed using AFLP as described by Katla et al. (10). The AFLP data were analyzed using PCA in Bionumerics software (Applied Maths BVBA, Belgium).

RESULTS

Eighty-nine strains of *L. monocytogenes* with different susceptibilities to sakacin P (10) were measured using FTIR spectroscopy and AFLP analysis. In addition, the 20 strains closest to the gap in sakacin P susceptibilities (10) were measured using Raman spectroscopy.

Analysis of FTIR and Raman spectra of the 20 strains closest to the gap in sakacin P susceptibilities. When PCA was used to analyze the 1,780-to-720-cm^{-1} range of the FTIR spectra of the respective 10 strains each from susceptibility groups A and B that are closest to the sakacin P susceptibility gap, the score plot showed that the 20 strains clustered in two groups, using a combination of PC1 and PC2 (Fig. 1). The strains in the two groups obtained corresponded to the strains in susceptibility groups A and B, with the exception of strain 762 (Table 1).

PLSR using the range from 1,780 to 720 cm^{-1} as x and an indicator variable for differentiation between the strains in susceptibility groups A and B as y was performed (PLSR model number 1). Evaluation of the PLSR score plot showed that strain 762 still clustered with strains from the other susceptibility group (results not shown). If the FTIR spectra of strain 762 were removed from the data set, PLSR resulted in a model where PLS component 1 separated perfectly between the two groups (PLSR model 2). For the latter model, the correlation coefficient was 0.98 and the optimal number of components was two.

Visual inspection of the regression coefficients from PLSR model 2 showed that certain spectral regions were more important than others for differentiating between the two susceptibility groups (Fig. 2). The regression coefficients were largest for the carbohydrate region (1,200 to 900 cm^{-1}), and most of the regression coefficients in this region were significant. For the fingerprint region (900 to 720 cm^{-1}), the regression coefficients were somewhat smaller, but most of them were significant for differentiation of the two groups. For the mixed region (1,500 to 1,200 cm^{-1}) and the protein region (1,700 to 1,500 cm^{-1}), the regression coefficients were small, and few of them were significant.

Using PLSR, it was also shown that the fatty acid region (3,000 to 2,800 cm^{-1}) of the FTIR spectra could be used to differentiate between the strains in susceptibility groups A and B (results not shown) (PLSR model 3). The resulting model had a correlation coefficient of 0.98, the number of components was four, and the score plot showed that a combination of PLS components 1 and 2 differentiated between the strains in susceptibility groups A and B.

When the Raman spectra (1,770 to 600 cm^{-1}) of the 20 strains were analyzed with PCA, the score plot showed that PC2 differentiated between the two groups of strains. Similar to the results obtained from PCA of the FTIR spectra, strain 762 clustered with strains from the other susceptibility group and was therefore left out of further data analysis.

The Raman spectra of the 19 remaining strains were used as input for a PLSR calculation where the spectral range from

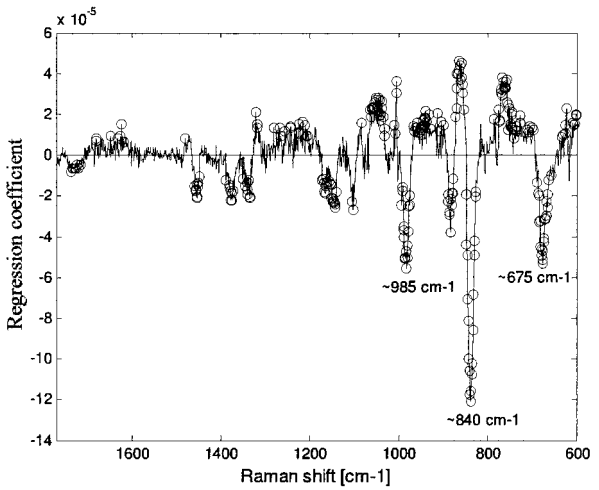

FIG. 3. Plot of regression coefficients from PLSR, with Raman spectra (1,770 to 600 cm^{-1}) of 20 strains of *Listeria monocytogenes* as *x* and an indicator variable for the differentiation of spectra from susceptibility groups A and B as *y* (PLSR model 4). Significant regression coefficients are marked with circles. Visual inspection of the *P* values showed that the bands at 985 cm^{-1}, 840 cm^{-1}, and 673 cm^{-1} were especially important for differentiation of the two susceptibility groups.

1,770 to 600 cm^{-1} was run as *x* and an indicator variable to differentiate between the strains in the two susceptibility groups was run as *y*. The strains in the two groups were separated by PLS component 1, the correlation coefficient from the regression was 0.98, and the optimal number of PLS components was three (PLSR model 4). The regression coefficients from the PLSR are plotted in Fig. 3. The figure shows that the range below 1,200 cm^{-1} contributed most to differentiation between Raman spectra for the strains in the two groups. The significant variables from the PLSR are also marked in the plot. Visual inspection of the *P* values indicated that three bands especially, namely 985 cm^{-1}, 840 cm^{-1}, and 675 cm^{-1}, were important in the PLSR (data not shown). When PLSR model 2 was reinvestigated with this in mind, it was seen that the bands at both 985 cm^{-1} and 840 cm^{-1} (Fig. 2) were among the significant bands for differentiation of the two susceptibility groups based on their FTIR spectra.

Grouping of all 89 *L. monocytogenes* strains based on their FTIR spectra. Above, it was shown that the strains closest to the sakacin P susceptibility gap could be differentiated into susceptibility groups A and B based on their FTIR spectra (Fig. 1). In order to investigate whether this separation could be extended to the 69 remaining strains, their FTIR spectra were used as inputs into PLSR model 2 in order to determine the grouping of these strains. The results showed that based on this model, the 69 remaining strains were divided into two distinct groups, which we called spectroscopy groups A and B (Table 1). The majority of strains in susceptibility group A were in spectroscopy group A, and the majority of strains in susceptibility group B were in spectroscopy group B. The exceptions were 12 of the strains in susceptibility group A and 2 of the strains in susceptibility group B, which fell in spectroscopy groups B and A, respectively.

Grouping of all 89 *L. monocytogenes* strains based on AFLP data. Analysis of the FTIR spectra showed that there was a consistent grouping of the 89 strains with respect to their chemical compositions. The grouping was investigated at the genetic level using AFLP analysis. The score plot from PCA of the AFLP data showed that the strains clustered in two groups, which we called AFLP group A and AFLP group B (Table 1). Most of the strains in susceptibility group A were in AFLP group A, and most of the strains in susceptibility group B were in AFLP group B. The exceptions were five of the strains from susceptibility group A and one of the strains from susceptibility group B, which fell into AFLP groups B and A, respectively.

DISCUSSION

Analysis of the FTIR and Raman spectra of the 20 *L. monocytogenes* strains closest to the sakacin P susceptibility gap showed that the strains in these two groups had different biochemical compositions and that the main variation in biochemical composition between the strains correlated with the variation in susceptibility to sakacin P. Based on this, it is tempting to suggest that the basis for the grouping of strains based on their FTIR spectra is related to the susceptibility to sakacin P.

The polysaccharide and fingerprint regions of the FTIR spectra were shown to be most important for differentiation of the strains in the two susceptibility groups. Bands from carbohydrates dominate the carbohydrate region, but there are also bands from nucleic acids (2) and phosphodiesters (14), for example, phospholipids. Analyses of both the FTIR and Raman spectra showed that two bands, at 985 cm^{-1} and 840 cm^{-1} (Fig. 2 and 3), were significant for differentiation of the two groups. According to Socrates (24), the bands at 985 cm^{-1} and 840 cm^{-1} can be attributed to pyranose. Pyranose, which is a collective term for six-member sugar rings, is abundant in the cell walls of all bacteria, for example, in the peptidoglycan sheet. Since the carbohydrate region of the FTIR spectra mainly consists of bands from the bacterial cell surface, this result indicates that at least some of the variation in susceptibility towards sakacin P in *L. monocytogenes* is coupled to variations in the bacterial cell wall, and perhaps more specifically, to variations in pyranose. The molecular basis for the difference in susceptibility to sakacin P for the two groups of *L. monocytogenes* is still not clear. However, it has previously been shown that the cell surface of *L. monocytogenes* is involved in the response to class II bacteriocins (26). More specifically, it has been suggested that the EII_t^{Man} permease, which is a transporter for glucose and mannose, also serves as a docking protein for class IIa bacteriocins in *L. monocytogenes* (5). After the bacteriocin has recognized the docking molecule, it may form pores in the bacterial membrane (6). It may be hypothesized that since different resistance levels to class II bacteriocins may be related to differences in the sugar transport apparatus, this could also have consequences for the composition of the carbohydrates in the cell wall as measured by FTIR and Raman spectroscopy. It should be noted, however, that none of the strains in the current study should be regarded as resistant towards bacteriocins since the susceptibility levels for the strains, as determined by Katla et al. (10), are much lower than those for strains resistant to bacteriocins.

Analysis of the FTIR spectra showed that the composition of

fatty acids varied for the strains in each of the two susceptibility groups and that variation in the proteins was small. This seems to be in contrast to an earlier study, where it was shown that the strains clustered according to sakacin P susceptibilities on the basis of sodium dodecyl sulfate-polyacrylamide gel electrophoresis data for whole-cell proteins, while clustering could not be achieved based on data from fatty acid analysis (10). The reason for the discrepancy with respect to the proteins might be that the clustering of the strains into two groups using the sodium dodecyl sulfate-polyacrylamide gel electrophoresis data was based on differences in rare proteins that are only a small part of the total protein content of the cell. For the fatty acid composition, no explanation for the discrepancy between the FTIR spectra and the fatty acid analysis has been found.

When all 89 *L. monocytogenes* strains were grouped based on their FTIR spectra or AFLP data, the resulting groups (spectroscopy groups A and B and AFLP groups A and B, respectively) corresponded well to susceptibility groups A and B. One explanation for this might be that the strains in each of the two groups have a specific mechanism for dealing with sakacin P. The reason why grouping based on the FTIR spectra and AFLP data did not correlate to the susceptibility groups for some strains is not known, but one explanation could be that these strains have more than one mechanism to reduce their susceptibility towards sakacin P. This corresponds to a previous report (26) which discussed that several mechanisms are probably involved in bacteriocin resistance in *L. monocytogenes*.

The 89 *L. monocytogenes* strains belong to either serogroup 1/2 or serogroup 4 (Table 1). Table 1 shows that there is a tendency that the strains with the lowest sensitivities to sakacin P are serogroup 1/2, while the strains with high sensitivities to sakacin P are both serogroup 1/2 and 4. Since the serology of *L. monocytogenes* is coupled to carbohydrate-containing proteins on the cell surface (20), this is in accordance with the observations from the FTIR and Raman spectra.

In conclusion, the variation in biochemical composition of *L. monocytogenes* strains, as determined by FTIR and Raman spectroscopy, correlated with the variation in susceptibility towards sakacin P. Analysis of the spectra indicated that the variation in the carbohydrates was most important, which may be connected to properties of the cell wall of the *L. monocytogenes* strains.

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